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**NATAL AND BREEDING DISPERSAL OF BOBOLINKS
(*DOLICHONYX ORYZIVORUS*) AND SAVANNAH SPARROWS
(*PASSERCULUS SANDWICHENSIS*) IN AN AGRICULTURAL LANDSCAPE**

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ABSTRACT.—Dispersal is a key process in the metapopulation dynamics and genetic structure of spatially segregated populations. However, our knowledge of avian dispersal, particularly in migratory passerines, remains limited. We studied dispersal of Bobolinks (*Dolichonyx oryzivorus*) and Savannah Sparrows (*Passerculus sandwichensis*) to determine whether agricultural management practices affected dispersal patterns and habitat selection. From 2002 to 2006, we banded adults and nestlings on six focal hay fields and two pastures in the Champlain Valley of Vermont and New York and searched for banded birds within 1.5 km of Vermont field sites during two years. Natal dispersal distances were greater than breeding dispersal in both species, and breeding dispersal distances of Bobolinks were greater than those of Savannah Sparrows. Site fidelity was high in both species, with >80% of detected adults and ~30% of detected natal dispersers returning to the same field in subsequent years. During natal dispersal, movement was random with respect to habitat quality. Adult Bobolinks dispersed to fields with annual reproductive rates greater than or equal to those of their original field; by contrast, adult Savannah Sparrows were more likely to move to or remain in low-quality habitats. During breeding dispersal, strong site fidelity took precedence over the effect of the previous year's nest success on the probability of dispersal, particularly for Savannah Sparrows. Site fidelity has implications for management of agricultural fields because consistency of cropping patterns and cutting dates are important for maintaining populations of these species. Received 14 June 2007, accepted 31 October 2008.

Key words: agricultural landscape, Bobolink, breeding, Champlain Valley, dispersal, *Dolichonyx oryzivorus*, habitat selection, natal, *Passerculus sandwichensis*, Savannah Sparrow.

Dispersión Natal y Reproductiva de *Dolichonyx oryzivorus* y *Passerculus sandwichensis* en un Paisaje Agrícola

RESUMEN.—La dispersión es un proceso clave que afecta la dinámica de metapoblaciones y la estructura genética de poblaciones segregadas espacialmente. Sin embargo, nuestro conocimiento de la dispersión de aves es limitado, particularmente para pájaros migratorios paserinos. Estudiamos la dispersión de *Dolichonyx oryzivorus* y *Passerculus sandwichensis* para determinar si las prácticas de manejo agrícola influyen sobre los patrones de dispersión y selección de hábitat. De 2002 a 2006, marcamos adultos y polluelos en seis campos de heno y dos potreros en el valle Champlain de Vermont y Nueva York, EE.UU., y buscamos pájaros marcados en un radio de 1.5 km alrededor de los campos de Vermont durante dos años. Las distancias de dispersión natal fueron mayores que las de dispersión reproductiva en las dos especies, y las distancias de dispersión reproductiva de *D. oryzivorus* fueron mayores que las de *P. sandwichensis*. La fidelidad al territorio fue alta en las dos especies, debido a que más del 80% de adultos encontrados y aproximadamente el 30% de los dispersores natales volvieron al mismo campo en años posteriores. El movimiento en la dispersión natal fue aleatorio con respecto a la calidad del hábitat. Los adultos *D. oryzivorus* se dispersaron a otros campos con tasas reproductivas anuales mayores o iguales a las de su campo original; en contraste, fue más probable que los adultos *P. sandwichensis* se movieran o se quedaran en hábitats de baja calidad. En la dispersión reproductiva, el efecto que el éxito reproductivo en años anteriores tuvo sobre la probabilidad de dispersión fue menor que la firme fidelidad al territorio, especialmente en *P. sandwichensis*. La fidelidad al territorio tiene implicaciones para el manejo de los campos agrícolas, porque la consistencia de los patrones de cultivo y las fechas de corte son importantes para mantener poblaciones de estas especies.

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BIRTH AND DEATH rates drive population dynamics in closed systems. However, few populations are truly closed, and migration rates must be quantified before population dynamics can be understood (Clobert et al. 2001). Collectively referred to as “dispersal,” movements of individuals among subpopulations are of critical importance for understanding the genetic structure of a population (Clark et al. 2004) and, where habitat quality varies spatially, source-sink dynamics (Pulliam 1988), and metapopulation dynamics (Levins 1970). It is also essential to consider dispersal in designing conservation reserves in fragmented landscapes (Walters 2000).

Despite its importance, our knowledge of dispersal remains incomplete. Population dynamics are highly sensitive to survival, but accurate assessment of this parameter is restricted by our inability to differentiate between dispersal and death. Similarly, our understanding of recruitment is hampered by the difficulty in discriminating between birth and immigration. Distinctions between these processes are particularly difficult in highly mobile species and habitats that show temporal variation in quality (Clark et al. 2004).

In resident birds, the process of dispersal occurs as a temporal continuum that usually terminates in the first six months of life (Morton et al. 1991). Once young are able to forage independently, extraterritorial forays lead to prospecting for territories, and finally to settlement, often within a few home ranges of their parents (Smith 1993, Baker et al. 1995). Dispersal data for migratory passerines are less common. Their selection of breeding sites is not apparent until they have migrated to non-breeding quarters and back (Morton et al. 1991), which makes tracking of passerines too small to carry satellite transmitters exceedingly difficult. Because many studies of passerine demography are sited in large expanses of suitable habitat, quantifying patterns of dispersal requires extraordinary search efforts. Although isotopic data are now being used to better assess population structure, base maps of isotopic variation reveal regional patterns rather than precise estimates of dispersal distances (e.g., Hobson 2002). One potential means of overcoming these problems is to use species that show restricted geographic distributions (e.g., Kirtland's Warbler [*Dendroica kirtlandii*]; Walker et al. 2003) or strict habitat requirements (e.g., Swainson's Thrush [*Catharus ustulatus*] in California; Johnson and Guepel 1996). In forested or suburbanizing ecosystems such as the northeastern United States, birds nesting in agricultural habitats may provide a model system in which to study dispersal processes because habitat options are relatively concentrated and limited in scale.

Grassland birds have shown range-wide population declines since the mid-1960s (Sauer et al. 2005). Demographic research on Bobolinks (*Dolichonyx oryzivorus*) and Savannah Sparrows (*Passerculus sandwichensis*) in the Champlain Valley (Vermont and New York) has shown that variation in management practices (hay date and frequency, grazing intensity) is the primary driver of mean annual reproductive rates for both species (Perlut et al. 2006). Given that numerous studies have found that individuals whose nests fail show a greater propensity for dispersal (Harvey et al. 1979, Gavin and Bollinger 1988, Haas 1998, Daniels and Walters 2000, Catlin et al. 2005), agricultural management may influence the probability of dispersal. Although variation in the probability, distance, and timing of dispersal has been linked to habitat quality (Lens and Dhondt 1994, Martin et al. 2007), social status (Pasinelli and Walters 2002, Pasinelli et al. 2004), sex

(Winkler et al. 2005, Stenzel et al. 2007), hatching date (Hansson et al. 2002), and prey availability (Byholm et al. 2003), we know little about the potential effects of agricultural management practices on this critical demographic parameter. In our study system, adults (consistently) and nestlings (occasionally) returned to breed at the previous year's breeding sites or near their place of birth; thus, these species may provide insights into dispersal patterns of small migratory songbirds. Additionally, the two species show differences in migratory strategies, with most Savannah Sparrows wintering in the continental United States and Bobolinks wintering in southern South America. In the present study, we quantified local-scale, between-year dispersal processes and habitat selection of Savannah Sparrows and Bobolinks in the Champlain Valley. Our goals were to (1) quantify dispersal patterns as a function of dispersal type (breeding versus natal), sex, and nest success in the previous year and (2) assess the role of agricultural management on patterns of dispersal and habitat selection.

METHODS

Study area.—The Champlain Valley supports a substantial dairy industry, with ~146,000 ha of managed grassland (National Agricultural Statistics Service 1999). We focused on four grassland management practices: (1) early-hayed fields (cut before 11 June and again in early to mid-July), (2) middle-hayed fields (cut between 21 June and 10 July), (3) late-hayed fields (cut after 1 August for bedding or forage for beef and dry cows), and (4) rotationally grazed pastures. Although fields are cut continuously from late May through August in this region, these time periods represent the actual cutting dates on our study sites and are correlated with distinct agricultural management objectives.

Three focal fields (minimum size = 10 ha) were located in Hinesburg, Vermont (late-hayed, pasture, and middle-hayed), three were located in Shelburne, Vermont (pasture, late-hayed, and early-hayed), and two were located in Cumberland Head-Beekmantown, New York (late-hayed and middle-hayed; Fig. 1). The Hinesburg focal fields were an average of 9 km east of the Shelburne study sites, and the New York fields were ~42 km north of the Shelburne fields. All focal fields were grass-dominated and actively used for agriculture (detailed vegetation and management descriptions in Perlut et al. 2006).

Field methods.—Early in the breeding season, we captured adult birds with mist nets placed systematically throughout the focal fields. As the breeding season progressed, unbanded birds were captured in mist nets placed near nests. Each captured adult was banded with a unique combination of one U.S. Fish and Wildlife Service (USFWS) aluminum band and three colored leg bands. Nestlings hatched in these fields received one metal USFWS band, generally at 6 days of age. In 2002–2006, using binoculars and a 15–60× scope, we searched for birds weekly on each of the eight focal study fields described above. In 2005 we searched systematically for banded birds within a 1.5-km radius around the three Shelburne focal fields (65 fields; 457 ha), and in 2006 we searched within a 1.5-km radius around all the Vermont focal fields (322 fields; 1,538 ha). Each field within the 1.5-km radii was visited on at least two different dates during the breeding season, between 0400 and 1300 hours EST, with an average search time of 2.5 h field⁻¹ (mean of 0.12 detections h⁻¹). No off-site searches were

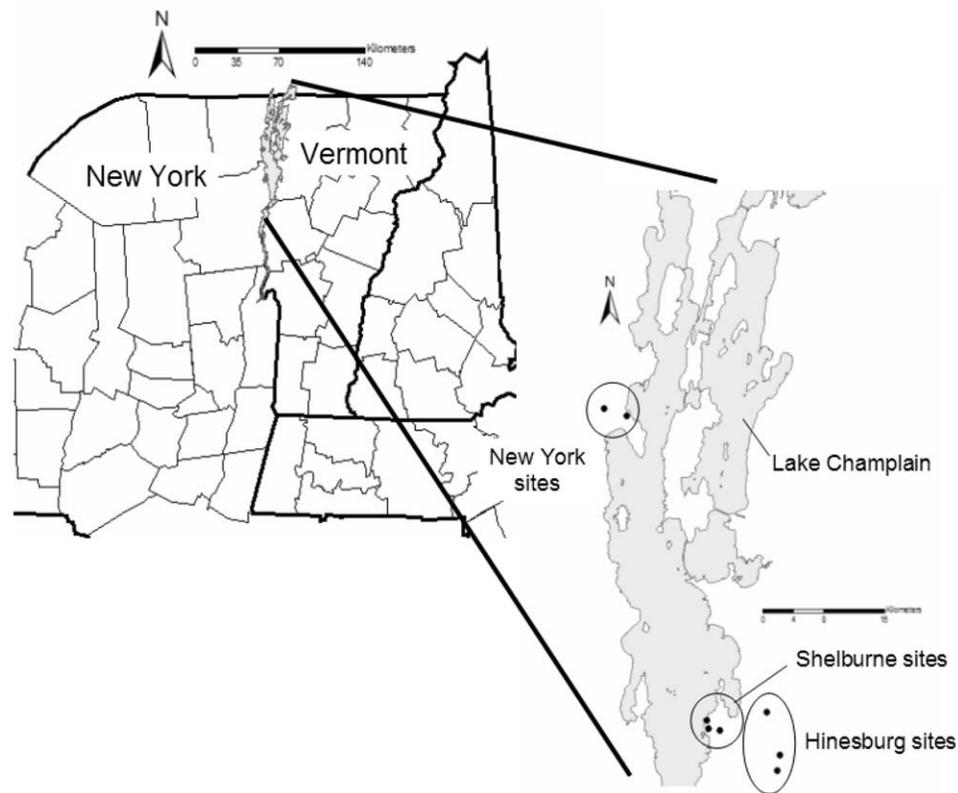


FIG. 1. The study area, Champlain Basin, Vermont and New York.

conducted on New York fields; therefore, New York data represented birds that either returned to the field in which they previously bred or dispersed between the two New York focal fields; no birds were documented to have dispersed across Lake Champlain (Fig. 1).

For the adults in Vermont, we estimated detection probability (p) using the Cormack-Jolly-Seber (Lebreton et al. 1992) method in the program MARK. In 2002–2004 (adults on focal fields in New York and Vermont), 2005 (adults on focal fields and within a 1.5-km radius of the Shelburne fields), and 2006 (adults on focal fields and within a 1.5-km radius of the Shelburne and Hinesburg fields), our model-averaged estimates of p were 0.70, 0.69, and 0.63, respectively (for additional details on model sets and parameters, see Perlut et al. 2008). Estimates of p were the same for both species. We could not estimate p for natal dispersers because of the small sample size; therefore, we did not use p to correct dispersal distances. However, our estimates of p suggest that although distance from the study site led to a bias in detection probability, this bias was not substantial.

All nest and resighting locations were recorded with a global positioning system (GPS) unit accurate to approximately 5–10 m. Using ARCMAP, version 9.1, and the Hawth's Tools extension, we calculated natal dispersal as the distance each bird moved from its nest to its point of capture. In some instances, resight or recapture did not occur in the year immediately following fledging; these events were still classified as "natal dispersal." Although natal dispersal distances were significantly greater than breeding dispersal distances (see below), this classification decision may have biased our estimates of natal dispersal distances.

For breeding dispersal, we measured the distance between a bird's final nest in year t to its first nest in year $t + 1$. If a bird was present but failed to nest or if its nest was not located in a given year, we used the center of the field as the point of origin. Fifty-two individuals returned to the same field but were not associated with a nest in either year, which resulted in dispersal distances of 0 m. As with natal dispersal, some birds ($n = 55$) were not resighted—recaptured in the year immediately following a known nesting attempt but were found in subsequent years. These events were also classified as "breeding dispersal." Because 46 of these 55 birds were relocated on the focal fields where they were originally banded, breeding dispersal distances for these birds were likely underestimated. We committed substantial effort to banding and nest searching on focal fields, so these birds likely moved to a different field in the intervening year(s).

We documented multiple breeding-dispersal events for some adults. Because these events may not be independent, we used only the first dispersal event for each individual. When all breeding-dispersal events were included in the analysis, the average dispersal distances changed by <10 m for both species. Birds became increasingly site-faithful after the first breeding-dispersal event, so analysis of subsequent changes in management choices was also largely irrelevant, given that management practices were consistent within fields among years. We documented both natal and breeding dispersal for seven Bobolinks and seven Savannah Sparrows. For these individuals, we classified their first dispersal event as "natal dispersal" and the second as "breeding dispersal."

TABLE 1. Descriptive statistics for natal and breeding dispersal in Savannah Sparrows and Bobolinks in the Champlain Valley of Vermont and New York, 2002–2006. Distances are recorded in meters.

Species	Dispersal type	Average (m)	Median (m)	SD	Maximum	<i>n</i>
Bobolink	Natal	1,522	975	2,025	8,424	31
Savannah Sparrow	Natal	913	885	690	2,825	36
Bobolink	Breeding	370	119	1,091	10,637	115
Savannah Sparrow	Breeding	113	63	198	2,009	226
						Σ = 408

Because the distance data were strongly skewed, we used Mann-Whitney *U*-tests to analyze the effects of sex, dispersal type, and species. For graphic interpretation, 300-m distance categories used in the analysis were based on average field configuration. Distances from field center to field perimeter were ~300 m; thus, species dispersing <300 m were typically returning to the same field. Distances between 300 and 600 m indicated moves to adjacent or nearby fields.

Field management.—To evaluate dispersal decisions in relation to habitat quality, we used data from Perlut et al. (2006, 2008). Here, mean annual birth and survival rates were lowest in early-hayed fields, followed by rotationally grazed pastures. For Bobolinks, birds in middle-hayed fields had lower reproductive rates than those in late-hayed fields, but Savannah Sparrows showed similar reproductive rates in middle- and late-hayed treatments. Thus, we pooled middle- and late-hayed fields for this analysis, because in both habitats the mean number of fledglings per female was greater than replacement levels (Perlut et al. 2006). We categorized dispersal moves as “favorable” when birds moved to or remained in high-quality habitat (i.e., middle- and late-hayed fields). “Unfavorable dispersal decisions” were defined as movement to habitats of lower quality or remaining in low-quality habitats (i.e., early-hayed and pasture). We calculated expected values for dispersal decisions as proportion of the search area in management type “origin” multiplied by the proportion in management type “destination.” Additionally, we assessed whether dispersal decisions were affected by nest success in the previous breeding season. “Nest success” was defined as ≥1 young fledged in a given breeding season, and “dispersal” (categorical variable: yes or no) was defined as movement to another field. This data set was smaller than that used for assessing dispersal distances and changes in management practices because this analysis required nest success in year *t* and dispersal data in year *t* + 1.

RESULTS

We recorded 408 dispersal events. For Savannah Sparrows, these data included breeding dispersal for 226 individuals (132 males and 94 females) and natal dispersal for 36 individuals (24 males, 11 females, and 1 of unknown sex). For Bobolinks, we recorded breeding dispersal for 115 individuals (56 males and 59 females) and natal dispersal for 31 individuals (16 males and 15 females; Table 1). Using estimates of apparent survival, breeding-dispersal observations accounted for 71.5% and 60.8% of expected survivors of Savannah Sparrows and Bobolinks, respectively. Natal-dispersal observations accounted for 16.1% and 22.7% of expected survivors of Savannah Sparrows and Bobolinks banded as nestlings, respectively (Table 2).

Dispersal distances.—The median natal dispersal distance was 975 m for Bobolinks (maximum = 8,424 m) and 885 m for Savannah Sparrows (maximum = 2,825 m; Table 1). There was no difference in natal dispersal distance between the two species ($U = 591$, $P = 0.68$). Approximately 30% of the natal-dispersal events resulted in individuals breeding in the field in which they were hatched (Table 2 and Fig. 2A). Most individuals dispersed <300 m or <900 m, which suggests that birds either returned to their natal field or moved a substantial distance from their birth site (Fig. 2A).

The mean breeding dispersal distances for Bobolinks (370 m; median = 119 m) were significantly greater than those for Savannah Sparrows (113 m; median = 63 m) ($U = 16,576$, $P < 0.001$). More than 80% of adults of both species returned to breed on the same field (Fig. 2B). Natal dispersal distances were greater than breeding dispersal distances in both species (both $U > 549$, both $P < 0.001$).

During breeding dispersal, male Savannah Sparrows moved significantly greater distances than females (Savannah Sparrow: female median = 50 m, male median = 78 m; $U = 7,211$, $P = 0.04$). We resighted substantially more males than females; thus, this

TABLE 2. Total numbers of Savannah Sparrows and Bobolinks banded as nestlings (natal) or adults (breeding) in 2002–2006 in the Champlain Valley of Vermont and New York and detected in subsequent years.

Dispersal type and species	Total banded	Expected number of detections ^a	Detected on same field	Detected on different field	Percentage of expected survivors detected ^b
Natal					
Savannah Sparrow	883	223	10	26	16.1
Bobolink	697	136	10	21	22.7
Breeding					
Savannah Sparrow	553	316	217	9	71.5
Bobolink	444	189	103	12	60.8

^aNumber for breeding dispersal calculated from apparent survival rates for each management type in Perlut et al. (2008). For natal dispersal, apparent survival rates were estimated as 44% of apparent survival rates for adults based on data from Swainson's Thrush (*Catharus ustulatus*; Gardali et al. 2003).

^bCalculated as (number detected on same field + number detected on different field)/expected number of detections.

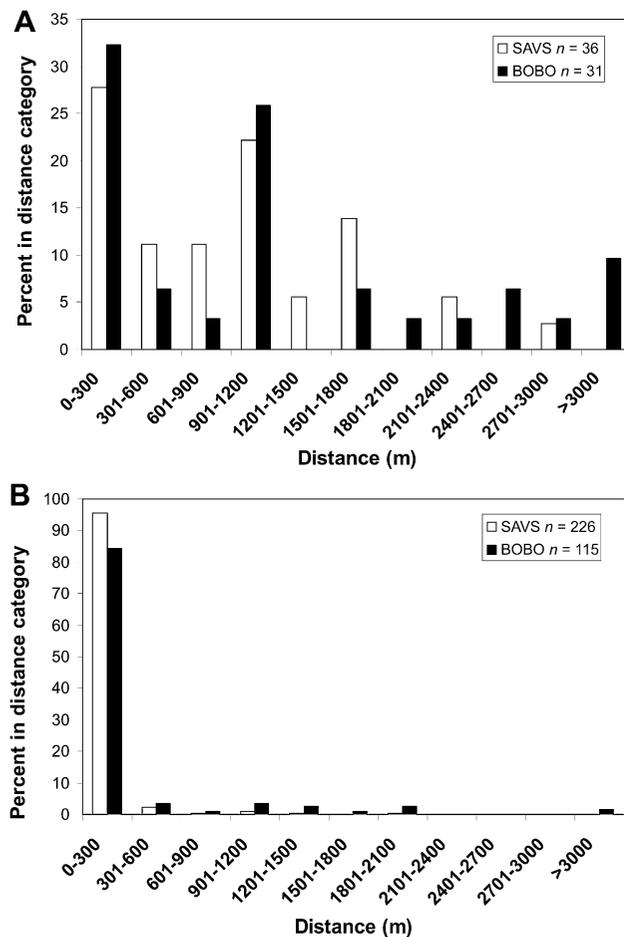


FIG. 2. Frequency distribution of (A) natal dispersal distances and (B) breeding dispersal distances of Savannah Sparrows (SAVS) and Bobolinks (BOBO) in the Champlain Valley, Vermont and New York, 2002–2006. Most individuals in the 0–300 category represent returns to the field in which they were hatched or nested the previous year.

result could be misleading if detection probabilities between sexes varied differentially by distance. We found no difference in breeding dispersal distances between male and female Bobolinks (Bobolink: female median = 129 m, male median = 108 m; $U = 1,856$, $P = 0.25$) or between sexes in either species during natal dispersal (Savannah Sparrow: female median = 552 m, male median = 885 m, $U = 110$, $P = 0.43$; Bobolink: female median = 361 m, male median = 1,033 m; $U = 115$, $P = 0.84$).

Habitat selection.—During natal dispersal, Savannah Sparrows showed no propensity to select fields with the same management treatment as their natal field ($\chi^2 = 2.04$, $df = 1$, $P = 0.15$; Table 3A). Additionally, natal dispersal was random with respect to management treatment, such that birds were equally likely to make favorable or unfavorable decisions with respect to habitat quality ($\chi^2 = 0.38$, $df = 1$, $P = 0.54$). Bobolinks were more likely to disperse to a field with the same management practice as their natal field ($\chi^2 = 5.24$, $df = 1$, $P = 0.02$; Table 3B); however, Bobolinks chose fields at random with respect to habitat quality ($\chi^2 = 0.91$, $df = 1$, $P = 0.34$), which is similar to the pattern found in Savannah Sparrows.

TABLE 3. Habitat selection during natal (A and B) and breeding (C and D) dispersal of Savannah Sparrows and Bobolinks in the Champlain Valley of Vermont and New York, 2002–2006. Cells with bold type indicate favorable choices, and cells with normal type indicate unfavorable choices. Note that because no Bobolinks fledged from early-cut fields, this row is not included as an option for origin in B.

(A) Savannah Sparrow, natal ($n = 36$)

		Destination		
		Early	Grazed	Middle and late
Origin	Early	3 (8.3%)	2 (5.6%)	3 (8.3%)
	Grazed	0 (0%)	2 (5.6%)	3 (8.3%)
	Middle and late	6 (16.7%)	3 (8.3%)	14 (38.9%)

(B) Bobolink, natal ($n = 31$)

		Destination		
		Early	Grazed	Middle and late
Origin	Grazed	0 (0%)	0 (0%)	1 (3.2%)
	Middle and late	8 (25.8%)	3 (9.7%)	19 (61.3%)

(C) Savannah Sparrow, breeding ($n = 226$)

		Destination		
		Early	Grazed	Middle and late
Origin	Early	64 (28.3%)	0 (0%)	5 (2.2%)
	Grazed	1 (0.4%)	52 (23.0%)	0 (0%)
	Middle and late	3 (1.3%)	0 (0%)	101 (44.7%)

(D) Bobolink, breeding ($n = 115$)

		Destination		
		Early	Grazed	Middle and late
Origin	Early	8 (7.0%)	0 (0%)	7 (6.1%)
	Grazed	1 (0.9%)	6 (5.2%)	2 (1.7%)
	Middle and late	1 (0.9%)	1 (0.9%)	89 (77.4%)

During breeding dispersal, both species showed strong selection for sites with similar management practices as their breeding site in the previous year (both $\chi^2 > 111$, $df = 1$, both $P < 0.001$; Table 3C, D). Preference for the same management practice in the subsequent year was a result of strong site fidelity, given that only 4 of 103 (Bobolink) and 6 of 217 (Savannah Sparrow) breeding-dispersal events were to different fields with the same management practices (Table 2).

Savannah Sparrows were more likely than expected to make unfavorable decisions with respect to management practices, with 120 of 226 (53%) moving to or remaining in low-quality habitats ($\chi^2 = 7.6$, $df = 1$, $P < 0.01$; Table 3A). By contrast, adult Bobolinks made favorable decisions more often than expected (98 of 115; $\chi^2 = 39.8$, $df = 1$, both $P < 0.001$; Table 3B).

Effects of nest success in the previous breeding season.—We recorded nest-success data and breeding-dispersal data in the subsequent breeding season for 87 Bobolinks and 150 Savannah Sparrows. Savannah Sparrows that nested successfully in one year (100 of 105, or 95%) were equally likely to return to breed on the same field in the following year as birds whose nests failed (40 of 45, or 89%; $\chi^2 = 2.04$, $df = 1$, $P = 0.15$). Only two (of five) birds that dispersed to a different field made favorable choices. Of the birds

that were successful, only 4.8% (5 of 105) dispersed to a different field the following year.

Bobolinks that nested successfully in one year (59 of 63, or 94%) were more likely to return to breed on the same field in the following year than birds whose nests failed (19 of 24, or 79%; $\chi^2 = 3.93$, $df = 1$, $P = 0.05$), which suggests an influence of nest success on site fidelity. Three (of five) birds that dispersed to a different field made favorable choices. Additionally, 4 (6.3%) of 63 birds that successfully fledged young dispersed to a different field in the following year.

Regardless of nest success, a greater proportion of adult Bobolinks made favorable decisions with respect to field-management practices. Eighty-six percent of Bobolinks (75 of 87) remained in or moved to higher-quality fields, whereas only 41% of Savannah Sparrows (61 of 150) did so.

DISCUSSION

Dispersal distances.—For both Savannah Sparrows and Bobolinks, natal dispersal distances were significantly greater than breeding dispersal distances and adults generally showed strong site fidelity. This pattern is expected, given that young or inexperienced birds typically move greater distances than adults (Clark et al. 2004) because of saturated habitats (Lens and Dhondt 1994), inbreeding avoidance (Greenwood 1980), and advantages of breeding philopatry (Wittenberger 1978).

We found evidence of differential breeding-dispersal distances between the sexes in Savannah Sparrows but not in Bobolinks. Many studies of avian dispersal have noted that females moved greater distances than males (Greenwood et al. 1979, Bollinger and Gavin 1989 [Bobolinks], Pärt 1990, Cilimburg et al. 2002, Forero et al. 2002), but greater male dispersal distances—the pattern we found in Savannah Sparrows—has been documented in other species (Alonso et al. 1998). Similar dispersal distances between sexes (Bull et al. 1988, Payne 1991) have been shown as well, including one study of Savannah Sparrows (Bédard and LaPointe 1984). Because females are less conspicuous during the breeding season, our detection rates may have been lower for females, or perhaps females were more likely to disperse >1.5 km.

The relatively modest natal dispersal distances we observed were ~4× greater than those documented for an island population of Savannah Sparrows, where the median natal dispersal distance was 228 m (Wheelwright and Mauck 1998). Our relatively high return rate for a mainland population of banded nestlings may be a function of the patchiness of grassland habitat in the Champlain Valley. In this region, grasslands are fragmented by forest, row crops (primarily corn), and other human developments, creating “islands” of habitat and constraining the range of choices for breeding sites. In a disjunct population of Bobolinks in Oregon, Wittenberger (1978) also found strong philopatry, with nearly one third of adults establishing territories within 50 m of where they held territories the previous year. Philopatry may be unavoidable in such circumstances (Wheelwright and Mauck 1998). These results contrast with those for Savannah Sparrows in Quebec, where breeding birds showed strong philopatry (48%) but no birds banded as nestlings returned to the study area (Bédard and LaPointe 1984). This population may be located in a region of greater habitat-homogeneity, though Bédard and LaPointe (1984) did not state this. A similar conclusion may be drawn from a study

of Savannah Sparrows in southeastern Michigan, in which only 1 young out of 130 banded returned to the study field (Potter 1972).

Our results of breeding philopatry and greater natal dispersal distances were comparable to results of other studies of grassland passerines. In a population of Horned Larks (*Eremophila alpestris*) in Colorado, 65% of adult birds returned to the same territories (Beason 1995). In Maine, 70% of Grasshopper Sparrows (*Ammodramus savannarum*) returned to within 200 m of territories occupied in the previous year, but only 2 of 19 banded nestlings returned to the same breeding locality (Vickery 1996). Only 1 of 46 Eastern Meadowlarks (*Sturnella magna*) banded as nestlings was resighted (960 m from natal site), whereas 8 of 14 adult males and 12 of 22 adult females returned to breed in the same area (Lanyon 1957). Similar patterns were found in Vesper Sparrows (*Pooecetes gramineus*); no banded nestlings ($n = 45$) were recaptured, whereas 46% of 24 banded breeding adults were recaptured at the banding site (Berger 1968).

Detection probability and biases in dispersal distances.—Koenig et al. (1996, 2000) suggested that without radiotelemetry or genetic data, estimates of dispersal distance will always be biased low because the probability of detecting long-distance dispersal events will always be less than that of detecting shorter-distance events. Two lines of evidence support the conclusion that our data are no exception to this pattern. First, as noted above, detection probabilities decreased with increases in the area searched. Second, using data presented in Figure 2A, we found a second “peak” of natal dispersers at 901–1,200 m, which is likely the result of a high detection probability for birds that dispersed between two pairs of study sites located ~1 km apart. For the first four distance categories (in raw numbers rather than percentages), we found 10, 4, 4, and 8 Savannah Sparrows and 10, 2, 1, and 8 Bobolinks, which suggests that detection probability for natal dispersers may be lower than our estimates for adults ($p = 0.6$ – 0.7). In studies of dispersal based on mark and recapture–resighting, resource limitations dictate the distance at which field personnel can search for marked birds. Thus, one of the recurring questions in any dispersal study revolves around the shape of the “tail.” Our data showed Bobolink dispersal >8 km and Savannah Sparrow dispersal to ~3 km; some proportion of our population likely dispersed greater distances than we were able to document. This is especially true for natal dispersal. Assuming that the juvenile survival rate is 44% of the adult survival rate (Gardali et al. 2003), we were able to locate only 16–23% of the birds that were expected to survive to breeding age. Thus, our sample represents only a portion of the potential dispersers, and we suggest prudence in interpreting these results.

Habitat selection.—Although dispersal distances provide a useful, standardized metric for comparison among species and landscapes, the more important metric for grassland songbirds in our study system is how their final dispersal destinations vary with respect to agricultural management practices. Dispersal distances may have minor consequences on reproductive output for species nesting in homogeneous landscapes. However, for grassland songbirds in agricultural landscapes, mean annual reproductive rates (Perlut et al. 2006) and apparent survival rates (Perlut et al. 2008) show significant differences among management practices. During breeding dispersal, a greater percentage of Bobolinks (86%) than of Savannah Sparrows (41%) made favorable decisions with respect to field-management practices.

This result is likely a direct consequence of the two species' responses to hay harvest, which serves to illustrate the greater site fidelity of Savannah Sparrows. In our study system, most Savannah Sparrows re-nested on the same field after cutting-induced nest failure, whereas 100% of Bobolinks dispersed (Perlut et al. 2006). This pattern of re-nesting allows Savannah Sparrows to achieve some degree of reproductive output on early-hayed fields, because some birds successfully fledge young after the first or second hay harvest. By contrast, the Bobolink fledging rate on early-hayed fields is essentially zero. Although quantitative estimates of site fidelity and behavioral response to cutting may not indicate a causal relationship, our data suggest that the two are likely inter-related. Past research has shown that Bobolinks that experienced poor breeding success in one year were less likely than successful birds to reoccupy the same site in following years (Martin 1974, Bollinger and Gavin 1989), which is similar to our results.

By contrast, neither species made favorable decisions during natal dispersal. Although data from Nova Scotia suggested that the presence of conspecifics is a cue used by recently fledged Bobolinks to assess potential breeding sites in subsequent years (Nocera et al. 2006), our data do not support this finding. Additionally, Perlut et al. (2008) showed that recruitment rates (birth + immigration) were greatest in early-cut fields, which implies that despite low reproductive success, these fields remain attractive to both species, and most likely to first-time breeders. If older males limit the ability of new recruits to colonize high-quality habitats through despotic interactions, carrying capacities may be imposed on middle- and late-hayed fields.

Of practical importance is how we can use these data to better understand the factors that influence habitat selection in agricultural landscapes. Strong site fidelity presents some difficulties to reversing population declines, though the manifestation of this life-history trait varies between species. The high site fidelity of Savannah Sparrows to all breeding habitats, regardless of quality, is problematic from a management perspective. Savannah Sparrows showed strong site fidelity to early-hayed fields where annual fledging rates for the population were less than replacement values. In Bobolinks, strong breeding-site fidelity to middle- and late-hayed fields (89 of 115 birds) suggests that once these birds find high-quality breeding sites, they tend to stay in those areas. The difference in migratory strategies between the two species may influence these decisions, given that Savannah Sparrows (short-distance migrants; Wheelwright and Rising 1993) have a longer nesting season than Bobolinks (long-distance migrants; Martin and Gavin 1995), which gives Savannah Sparrows greater flexibility in their choice of nesting habitats.

Management implications.—The strong site fidelity demonstrated in adults of both species may constrain their ability to select fields that would provide greater reproductive success, but it provides an opportunity for land managers to designate areas of high-quality habitat for conservation efforts, given that breeding adults are likely to return to the same fields in subsequent years. Thus, consistent management practices over time will allow managers and landowners to create high-quality habitat for breeding Savannah Sparrows and Bobolinks. This can occur not only through maintenance of long-term source habitat (i.e., middle- and late-hayed fields) but also by enabling some birds, primarily Bobolinks, to disperse (either between or within years)

from low-quality habitats (i.e., early-cut and grazed fields). Fields managed for several years as late-hayed and changed to early-hayed or pasture could have severe negative effects on songbirds' reproductive success. Dale et al. (1997) suggested delaying haying until after 15 July, by which time $\geq 70\%$ of nestlings will have fledged in years of normal breeding phenology. This corresponds to results obtained on our study sites (Perlut et al. 2006). Because forage protein levels peak early in the growing season (before mid-June), delayed mowing on productive hay fields is impracticable for most farmers (Cherney et al. 1993). However, we recommend that farmers and other landowners who need to cut during the breeding season set aside a small portion of their land (e.g., wet sites or sites with poor soils) to be cut after mid-July. There are government programs in place (e.g., the Wildlife Habitat Incentives Program; see Acknowledgments) that give financial incentives to farmers and landowners who set land aside for wildlife conservation efforts.

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LITERATURE CITED

- ALONSO, J. C., E. MARTIN, J. A. ALONSO, AND M. B. MORALES. 1998. Proximate and ultimate causes of natal dispersal in the Great Bustard *Otis tarda*. *Behavioral Ecology* 9:243–252.
- BAKER, M., N. NUR, AND G. R. GEUPEL. 1995. Correcting biased estimates of dispersal and survival due to limited study area: Theory and an application using Wrentits. *Condor* 97:663–674.
- BEASON, R. C. 1995. Horned Lark (*Eremophila alpestris*). In *The Birds of North America*, no. 195 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- BÉDARD, J., AND G. LAPOINTE. 1984. Banding returns, arrival times, and site fidelity in the Savannah Sparrow. *Wilson Bulletin* 96:196–205.
- BERGER, A. J. 1968. Vesper Sparrow. Pages 868–886 in *Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and their allies*, part 2 (O. L. Austin, Ed.). U.S. National Museum Bulletin, no. 237.
- BOLLINGER, E. K., AND T. A. GAVIN. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. *Auk* 106:584–594.

- BULL, E. L., M. G. HENJUM, AND R. S. ROHWEDER. 1988. Home range and dispersal of Great Gray Owls in northeastern Oregon. *Journal of Raptor Research* 22:101–106.
- BYHOLM, P., P. SAUROLA, H. LINDÉN, AND M. WIKMAN. 2003. Causes of dispersal in Northern Goshawks (*Accipiter gentilis*) in Finland. *Auk* 120:706–716.
- CATLIN, D. H., D. K. ROSENBERG, AND K. L. HALEY. 2005. The effects of nesting success and mate fidelity on breeding dispersal in Burrowing Owls. *Canadian Journal of Zoology* 83:1574–1580.
- CHERNEY, D. J. R., J. H. CHERNEY, AND R. F. LUCEY. 1993. *In vitro* digestion kinetics and quality of perennial grasses as influenced by forage maturity. *Journal of Dairy Science* 76:790–797.
- CILIMBURG, A. B., M. S. LINDBERG, J. J. TEWKSBURY, AND S. J. HEJL. 2002. Effects of dispersal on survival probability of adult Yellow Warblers (*Dendroica petechia*). *Auk* 119:778–789.
- CLARK, R. G., K. A. HOBSON, J. D. NICHOLS, AND S. BEARHOP. 2004. Avian dispersal and demography: Scaling up to the landscape and beyond. *Condor* 106:717–719.
- CLOBERT, J., E. DANCHIN, A. A. DHONDT, AND J. D. NICHOLS. 2001. *Dispersal*. Oxford University Press, Oxford, United Kingdom.
- DALE, B. C., P. A. MARTIN, AND P. S. TAYLOR. 1997. Effects of hay management on grassland songbirds in Saskatchewan. *Wildlife Society Bulletin* 25:616–626.
- DANIELS, S. J., AND J. R. WALTERS. 2000. Between-year breeding dispersal in Red-cockaded Woodpeckers: Multiple causes and estimated cost. *Ecology* 81:2473–2484.
- FORERO, M. G., J. A. DONÁZAR, AND F. HIRALDO. 2002. Causes and fitness consequences of natal dispersal in a population of Black Kites. *Ecology* 83:858–872.
- GARDALI, T., D. C. BARTON, J. D. WHITE, AND G. R. GEUPEL. 2003. Juvenile and adult survival of Swainson's Thrush (*Catharus ustulatus*) in coastal California: Annual estimates using capture–recapture analyses. *Auk* 120:1188–1194.
- GAVIN, T. A., AND E. K. BOLLINGER. 1988. Reproductive correlates of breeding-site fidelity in Bobolinks (*Dolichonyx oryzivorus*). *Ecology* 69:96–103.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- GREENWOOD, P. J., P. H. HARVEY, AND C. M. PERRINS. 1979. The role of dispersal in the Great Tit (*Parus major*): The causes, consequences and heritability of natal dispersal. *Journal of Animal Ecology* 48:123–142.
- HAAS, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: An experimental approach. *Auk* 115:929–936.
- HANSSON, B., S. BENSCH, AND D. HASSELQUIST. 2002. Predictors of natal dispersal in Great Reed Warblers: Results from small and large census areas. *Journal of Avian Biology* 33:310–314.
- HARVEY, P. H., P. J. GREENWOOD, AND C. M. PERRINS. 1979. Breeding area fidelity of Great Tits (*Parus major*). *Journal of Animal Ecology* 48:305–313.
- HOBSON, K. A. 2002. Incredible journeys. *Science* 295:981–983.
- JOHNSON, M. D., AND G. R. GEUPEL. 1996. The importance of productivity to the dynamics of a Swainson's Thrush population. *Condor* 98:133–141.
- KOENIG, W. D., P. N. HOOGE, M. T. STANBACK, AND J. HAYDOCK. 2000. Natal dispersal in the cooperatively breeding Acorn Woodpecker. *Condor* 102:492–502.
- KOENIG, W. D., D. VAN VUREN, AND P. N. HOOGE. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution* 11:514–517.
- LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publications of the Nuttall Ornithological Club, no. 1.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62:67–118.
- LENS, L., AND A. A. DHONDT. 1994. Effects of habitat fragmentation on the timing of Crested Tit *Parus cristatus* natal dispersal. *Ibis* 136:147–152.
- LEVINS, R. 1970. Extinction. Pages 77–107 in *Some Mathematical Problems in Biology* (M. Gesternhaber, Ed.). American Mathematical Society, Providence, Rhode Island.
- MARTIN, J., W. M. KITCHENS, AND J. E. HINES. 2007. Natal location influences movement and survival of a spatially structured population of Snail Kites. *Oecologia* 153:291–301.
- MARTIN, S. G. 1974. Adaptations for polygynous breeding in the Bobolink, *Dolichonyx oryzivorus*. *American Zoologist* 14:109–119.
- MARTIN, S. G., AND T. A. GAVIN. 1995. Bobolink (*Dolichonyx oryzivorus*). In *The Birds of North America*, no. 176 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- MORTON, M. L., M. W. WAKAMATSU, M. E. PEREYRA, AND G. A. MORTON. 1991. Postfledging dispersal, habitat imprinting, and philopatry in a montane, migratory sparrow. *Ornis Scandinavica* 22:98–106.
- NATIONAL AGRICULTURAL STATISTICS SERVICE. 1999. 1997 Census of Agriculture. [Online.] Available at www.agcensus.usda.gov/Publications/1997/index.asp.
- NOCERA, J. J., G. J. FORBES, AND L. -A. GIRALDEAU. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. *Proceedings of the Royal Society of London, Series B* 273:349–355.
- PÄRT, T. 1990. Natal dispersal in the Collared Flycatcher: Possible causes and reproductive consequences. *Ornis Scandinavica* 21: 83–88.
- PASINELLI, G., K. SCHIEGG, AND J. R. WALTERS. 2004. Genetic and environmental influences on natal dispersal distance in a resident bird species. *American Naturalist* 164:660–669.
- PASINELLI, G., AND J. R. WALTERS. 2002. Social and environmental factors affect natal dispersal and philopatry of male Red-cockaded Woodpeckers. *Ecology* 83:2229–2239.
- PAYNE, R. B. 1991. Natal dispersal and population structure in a migratory songbird, the Indigo Bunting. *Evolution* 45:49–62.
- PERLUT, N. G., A. M. STRONG, T. M. DONOVAN, AND N. J. BUCKLEY. 2006. Grassland songbirds in a dynamic management landscape: Behavioral responses and management strategies. *Ecological Applications* 16:2235–2247.
- PERLUT, N. G., A. M. STRONG, T. M. DONOVAN, AND N. J. BUCKLEY. 2008. Grassland songbird survival and recruitment in agricultural landscapes: Implications for source–sink demography. *Ecology* 89:1941–1952.
- POTTER, P. E. 1972. Territorial behavior in Savannah Sparrows in southeastern Michigan. *Wilson Bulletin* 84:48–59.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.

- SAUER, J. R., J. E. HINES, AND J. FALLON. 2005. The North American Breeding Bird Survey, Results and Analysis 1966–2004, version 2005.2. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland.
- SMITH, S. M. 1993. Black-capped Chickadee (*Parus atricapillus*). In *The Birds of North America*, no. 39 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- STENZEL, L. E., G. W. PAGE, J. C. WARRINER, J. S. WARRINER, D. E. GEORGE, C. R. EYSTER, B. A. RAMER, AND K. K. NEUMAN. 2007. Survival and natal dispersal of juvenile Snowy Plovers (*Charadrius alexandrinus*) in central coastal California. *Auk* 124:1023–1036.
- VICKERY, P. D. 1996. Grasshopper Sparrow (*Ammodramus sava-narum*). In *The Birds of North America*, no. 239 (A. Poole and F. Gill, Eds.). *Birds of North America*, Philadelphia.
- WALKER, W. S., B. V. BARNES, AND D. M. KASHIAN. 2003. Landscape ecosystems of the Mack Lake burn, northern Lower Michigan, and the occurrence of the Kirtland's Warbler. *Forest Science* 49:119–139.
- WALTERS, J. R. 2000. Dispersal behavior: An ornithological frontier. *Condor* 102:479–481.
- WHEELWRIGHT, N. T., AND R. A. MAUCK. 1998. Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah Sparrows. *Ecology* 79:755–767.
- WHEELWRIGHT, N. T., AND J. D. RISING. 1993. Savannah Sparrow (*Passerculus sandwichensis*). In *The Birds of North America*, no. 45 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- WINKLER, D. W., P. H. WREGE, P. E. ALLEN, T. L. KAST, P. SENESAC, M. F. WASSON, AND P. J. SULLIVAN. 2005. The natal dispersal of Tree Swallows in a continuous mainland environment. *Journal of Animal Ecology* 74:1080–1090.
- WITTENBERGER, J. F. 1978. The breeding biology of an isolated Bobo-link population in Oregon. *Condor* 80:355–371.

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